

THE BIOLOGY AND FUNCTIONAL MORPHOLOGY OF *LATERNULA TRUNCATA* (LAMARCK 1818) (BIVALVIA: ANOMALODESMATA: PANDORACEA)

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The subdivision of the class Bivalvia has been and still is, a source of controversy. Most systematists agree that the Protobranchia are distinct from the Lamellibranchia (Ridewood, 1903; Pelseneer, 1911; Owen, 1959; Purchon, 1959; Yonge, 1959; J. E. Morton, 1967). On the other hand the scavenging Septibranchia (Yonge, 1928) are considered by some authorities, *e.g.*, Purchon (1962) to be derivable directly from a protobranch ancestor. Alternatively some early workers (Ridewood, 1903; Douvillé, 1912) and the majority of present day authorities, *e.g.*, Newell (1965); J. E. Morton (1967) and Taylor, Kennedy and Hall (1972) regard the septibranchs as being highly specialized members of the Lamellibranchia. In such classification schemes they have usually been ordered with a group of highly specialized lamellibranchs, the so-called Anatinacea, in the sub-order (Thiele, 1935) or sub-class (Newell, 1965) Anomalodesmata. J. E. Morton (1967) puts the Septibranchia (Poromyacea) in the same class as, but in a different order from, the remaining "Anatinacea," the Pandoracea and Clavagellacea.

Most modern authorities agree on the classification scheme proposed by Newell (1965), *e.g.*, Taylor, *et al.* (1972) in which the sub-class Anomalodesmata is divided into four Super-families, the rare Pholadomyacea, the Pandoracea (including *Laternula*), the Poromyacea (the septibranchs) and the Clavagellacea. This scheme of classification has been adopted in this paper.

The Poromyacea are not well known, the most adequate account of two of them, *i.e.*, *Cuspidaria* and *Poromya* being by Yonge (1928). Little is known about the Pholadomyacea (Runnegar, 1972) and only *Brechites penis* in the Clavagellacea having been studied in any great detail by Purchon (1956, 1960), although Soliman (1971) has recently reported upon a species of *Clavagella*.

The Pandoracea are the best known, such genera as *Pandora* and *Cochlodesma* having been studied by Allen (1945, 1958) and *Entodesma* and *Mytilimeria* by Yonge (1952). In relative terms, however, this assemblage too is poorly known. For this reason a detailed study has been undertaken of *Laternula truncata* (Lamarck 1818).

MATERIALS AND METHODS

Specimens of *Laternula truncata* were collected from various sites in Hong Kong at irregular intervals. One of the better collecting sites was Tai Po marshes in Tolo Harbour.

Specimens for routine serial sectioning were fixed in alcoholic Bouin Duboscq and stained in either Heidenhain's haematoxylin, Masson's trichrome or Mallory's triple stain.

Portions of the ctenidial filaments and the style sac, were treated in the same way and sectioned transversely.

Portions of the digestive diverticula and of the kidney were also fixed in Zenker's fixative and subsequently stained in Heidenhain's hematoxylin.

Five optic tentacles were fixed in Zenker's fixative and stained in Heidenhain's hematoxylin while a further five were fixed in 5% formal saline and stained for nervous tissue by Holme's silver method (Carleton and Drury, 1957). Half of the eyes were sectioned transversely, the remainder longitudinally.

The ciliary currents elucidated in this work were demonstrated by the application of suspended carmine particles in sea water.

RESULTS

Ecology

The Anomalodesmata comprise a diverse assemblage of bivalves which are generally adapted to infaunal life. They occur sublittorally, *e.g.*, *Thracia* (Yonge, 1937), at low tide on muddy shores, *e.g.*, *Pandora* (Allen, 1954), *Brechites* (Purchon, 1956, 1960) and under stones on the shore, *e.g.*, *Entodesma* (Yonge, 1952). *Mytilimeria* is adapted to a highly specialized mode of life embedded in the tests of ascidians (Yonge, 1952). *Lyonsia* (Ansell, 1967), *Mytilimeria* and *Entodesma* (Yonge, 1952) possess a byssus. *Cuspidaria* and *Poromya* are members of the infaunal benthos (Yonge, 1928). Some clavagellids are found in soft rocks and corals (Soliman, 1971).

In the Periplomatidae, *Cochlodesma* (Allen, 1958) occurs in fine gravels from extreme low water mark to a depth of 60 fathoms. Vohra (1971) has recently shown that *Laternula anatina* occurs on sandy shores at all levels except the uppermost ones. I have found *Laternula tasmanica* over a wide range of tidal levels on the sandy shores of New South Wales, Australia although the animal is particularly prevalent in estuarine sands and is most commonly found burrowing in *Zostera* beds. Purchon (1958) reported *Laternula rostrata* (= *Laternula truncata*) as occurring on the seaward side of mangrove formations in Singapore. This is also the habitat occupied by this species in Hong Kong, although it has only been found on shores of coarse sand, *e.g.*, Tai Po marshes in Tolo Harbour. In Deep Bay, where there is a muddy shore on the seaward side of the mangroves, *L. truncata* is only found in localized patches of coarse sand or gravel. As far as is known from the available records *L. truncata* is distributed from Japan in the North (Kira, 1962) to Singapore in the South (Purchon, 1958).

Unlike *Thracia* (Yonge, 1937) and *Cochlodesma* (Allen, 1958), the species of *Laternula* upon which we have information do not build true burrows. They are always found lying vertically in the sand with the siphons pointing upwards. *Cochlodesma* lies horizontally (Allen, 1958). A large specimen of *L. truncata*, *i.e.*, of shell length of 6 cm, would be found at a depth of 9 cm, the siphons extending to the surface. When dug up, the animal showed no escape reactions, indeed in nearly all cases the siphons were not withdrawn. Once disturbed, the adult animal is incapable of reburrowing; the foot being small and of no use in this respect. This observation was subsequently verified in the laboratory. *L. truncata* can be regarded as a "passive burrower" as *Pholadomya* is assumed to be (Runnegar, 1972). Siphonal retraction is always very slow.

Young specimens of *L. truncata* (and *L. tasmanica*) possess a relatively large, mobile foot and the animal can burrow when disturbed.

Functional morphology

The shell and ligament. The shell of *Laternula truncata* is inequivalve, the left valve being somewhat deeper than the right and overlapping it slightly. The shell valves are markedly inequilateral. The anterior region of the shell is enlarged, whilst the posterior region is narrower and elongated, housing the long siphons when they contract (Fig. 1). There is a deep and broad pallial sinus (PS) to the pallial line (PL). The pallial line is wide.

The shell is pearly white in color both internally and externally, particularly in the dorsal region of the shell where much of the calcareous material has been eroded away perhaps due to the acid mangal soil (Macnae, 1968). Marginally a wide band of thinly distributed calcareous material is present. Taylor, *et al.* (1972) have shown that all of the Pandoracea (except the Thracidae) have a char-

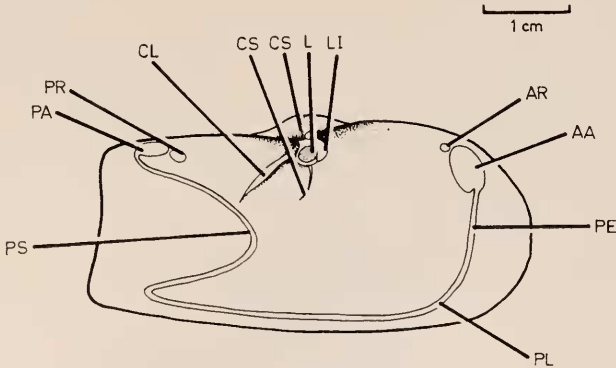


FIGURE 1. *Laternula truncata*, interior view of the left shell valve. Abbreviations are: AA, Anterior adductor muscle scar; AR, Anterior pedal retractor muscle scar; CL, Clavicle; CS, Crack in shell; L, Ligament; LI, Lithodesma; PA, Posterior adductor muscle scar; PE, Pedal gape; PL, Pallial line; PR, Posterior pedal retractor muscle scar; PS, Pallial sinus.

acteristic shell microstructure of inner and middle nacreous layers and a thinly distributed outer prismatic layer. Conditions in *L. truncata* are similar.

The periostracal layer is brown in color and rough in texture. Marginally it is thick, although over the rest of the shell it is thin. Dorsally, on either side of the primary ligament the periostracum of the left and right sides fuses uniting the shell valves in these regions (Fig. 2, FP). A similar situation has been reported for *Pandora* and *Cochlodesma* (Allen 1954; 1958) and *Entodesma* and *Mytilimeria* (Yonge, 1952).

When closed the shell valves only meet mid-ventrally and mid-dorsally at the ligament. There is a small anterior pedal gape (PE) and an extensive posterior siphonal gape.

The overall dimensions of the shell of *L. truncata* are comparatively regular as can be seen from the estimate of the ratio of width:height:length which is

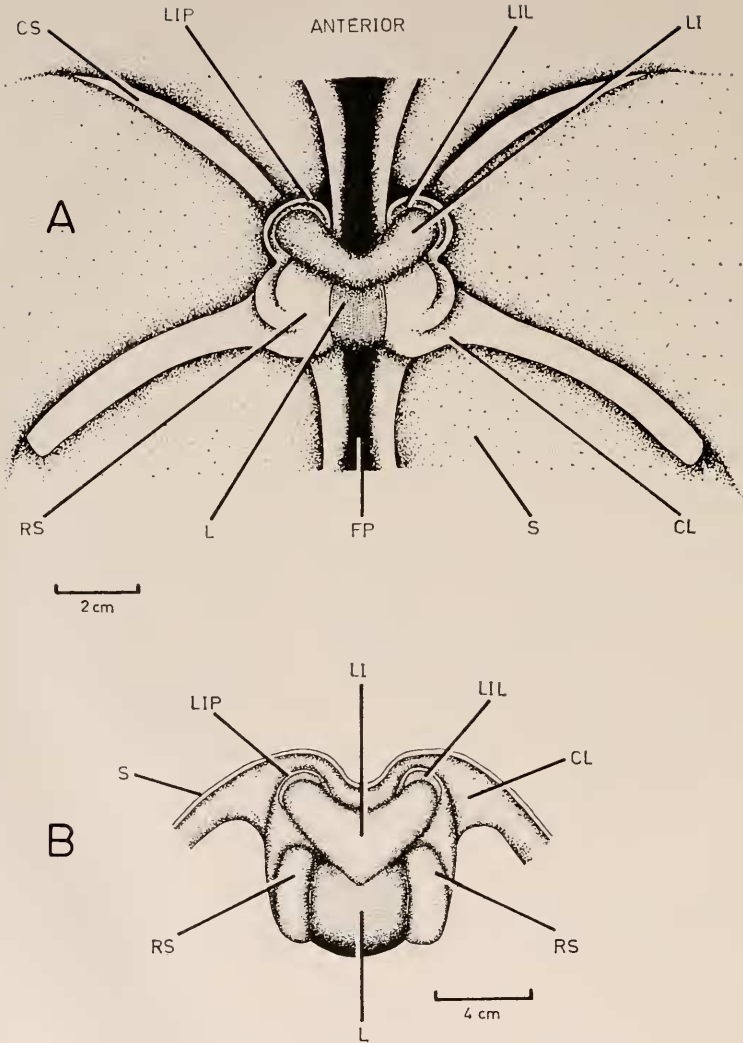


FIGURE 2. *Laternula truncata*, the ligament and lithodesma viewed from (A) the ventral and (B) from the anterior aspect. Abbreviations are: CL, Clavicle; CS, Crack in shell; FP, Fused periostracum; L, Ligament; LI, Lithodesma; LIL, Lithodesmal ligament; LIP, Lithodesmal plate; RS, Resilifer; S, Shell.

1:1.31 \pm 0.19:3.18 \pm 0.56. These figures suggest that shell length is one of the most variable factors in the growth of the shell. The shell is thin. The largest specimen of *L. truncata* examined had dimensions of: width 1.90 cm, height 2.60 cm, length 6.0 cm, and a shell thickness of, mid anteriorly, only 0.2 mm. This is due to the reduction of the prismatic layer of the shell.

A crack in each shell valve (Figs. 1 and 2, CS) extends ventrally from the umbo to approximately half the height of the shell. The anterior edge of the

crack overlies the posterior edge, thereby preventing entry of terrigenous material, but at the same time allowing the bending of the dorsal border of the shell, when the adductor muscles contract.

The ligament (Fig. 2, L) of *L. truncata* is small and is located on a resilifer (RS) from which also radiate laterally the posterior major shell supporting struts or clavicles (CL) which serve to strengthen the thin shell. Anterior to, and fused to, the ligament is a boomerang shaped calcareous ossicle, or lithodesma (LI), which is also attached by ligamental pads (LIL) to the lithodesmal plates (LIP) of the resilifer. The lithodesma effectively prevents expansion of the ligament when the adductor muscles relax. A lithodesma, though of different shapes, is also found in *Myodora*, *Myochama* and *Chamostrea* (Thiele, 1935) and in *Mytilimeria* and *Entodesma* (Yonge, 1952). The ligament of the periplomatid *Cochlodesma praetenu* has been described by Allen (1958, 1960) as being unusual in form but basically opisthodontic. Surprisingly Allen did not notice that a large lithodesma

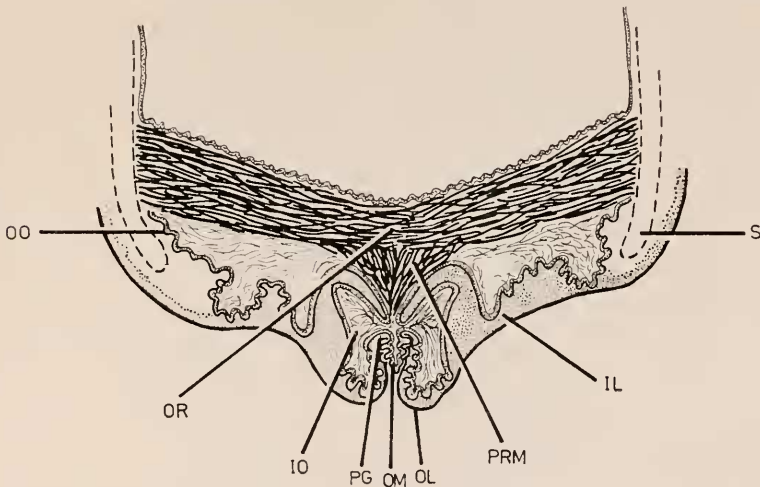


FIGURE 3. *Laternula truncata*, a transverse section through the ventral mantle margin. Abbreviations are: IL, Inner periostracal layer; IO, Inner layer of outer mantle fold; OL, Outer periostracal layer; OM, Fused outer layers of middle mantle fold; OO, Outer layer of outer mantle fold; OR, Orbital muscle; PG, Periostracal groove; PRM, Pallial retractor muscle; S, Shell.

is present in this species. The ligament of *L. truncata* is very similar to that of *Cochlodesma*.

The mantle. Fusion of the marginal folds of the mantle occurs dorsally above the exhalant siphon and also anterior to the pedal gape. In these regions the fusion is by way of the inner and middle folds and the inner surfaces of the outer folds and is thus of type C (Yonge, 1957). Such an arrangement accounts for the fusion of the periostracum already alluded to in this region and which forms a secondary "external" ligament. Such a situation was originally regarded by Owen Trueman and Yonge (1953) as primitive, but subsequently Yonge (1957), at least, changed his mind, and considered this feature to be secondary.

Ventrally, that is between the inhalant siphon and the pedal gape, mantle fusion involves only the inner folds and the inner surfaces of the middle mantle folds and is thus of type B (Yonge, 1957) (Fig. 3). Such a condition is not, apparently, characteristic of the Anatinacea studied earlier by Yonge (1952, 1957) in which all mantle fusion is apparently of type C. In *Laternula truncata* anterior and posterior to the mid point of the ventral border the fusion gradually involves the outer surfaces of the middle mantle folds and the inner surfaces of the outer mantle folds to give the type C condition, described above.

There is a small pedal aperture located antero-ventrally, but there is no fourth pallial aperture in *L. truncata* as there is in *Entodesma* and *Mytilimeria* (Yonge, 1952).

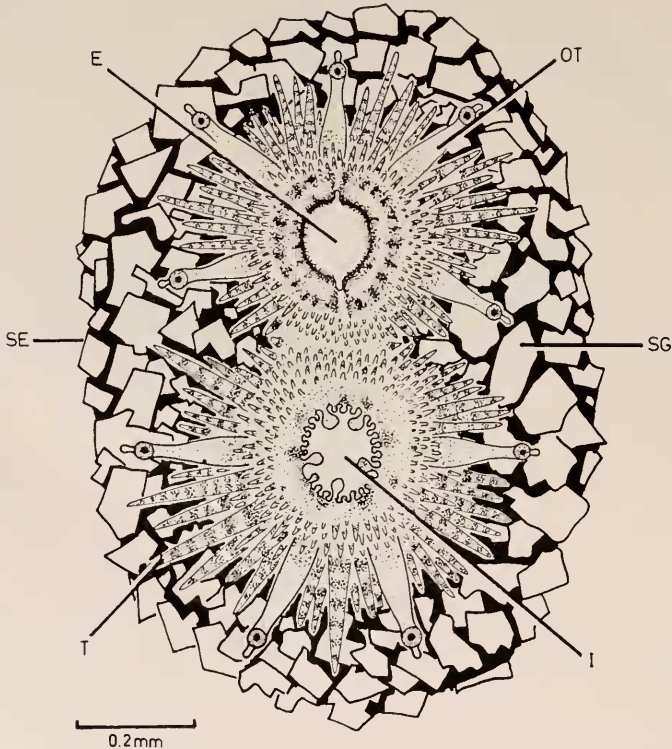


FIGURE 4. *Laternula truncata*, a posterior view of the siphons with the animal actively filtering fresh sea water. Abbreviations are: E, Exhalant siphon; I, Inhalant siphon; OT, Optic tentacle; SE, Siphonal edge; SG, Sand grains; T, tentacle.

The periostracum is composed of two layers. The outer layer (OL) is thin ($2.5\text{--}5.0\ \mu$) and stains bright red with Masson's trichrome and Mallory's triple stain. The inner layer (IL) stains bright blue with both of these stains and as noted earlier is very thick marginally ($50\text{--}100\ \mu$). In other regions of the shell, however, this layer is thin ($10\ \mu$). It is secreted by the inner surface of the outer mantle fold (IO). A similar two layered periostracum is also found in *Dreissena polymorpha* (B. S. Morton, 1969) and *Galeomma takii* (B. S. Morton,

1973b) though the situation is more complicated in various mytilid genera (Beedham, 1958; B. S. Morton, 1973a) where the periostracum is composed of three layers.

The mantle is exceptionally thin over the general surface, except ventrally where it contains muscles which unite the valves and which can be referred to as orbital muscles (OR). Pallial retractors (PRM) serve to withdraw the mantle margins into the shell, presumably when the animal is disturbed. The occurrence of such large muscles uniting the two valves accounts for the wide pallial line and suggests that these muscles may be important in movement of the shell valves. Orbital muscles are also well developed in the Saxicavacea (Russell Hunter, 1949; Yonge, 1971).

The siphons. The combined siphons of *Laternula truncata* when fully extended are almost half as long as the shell and are formed by fusion of all three folds of the mantle margin including the periostracal groove and are thus of type C (Yonge, 1957). The thick periostracum that surrounds them is covered by sand grains

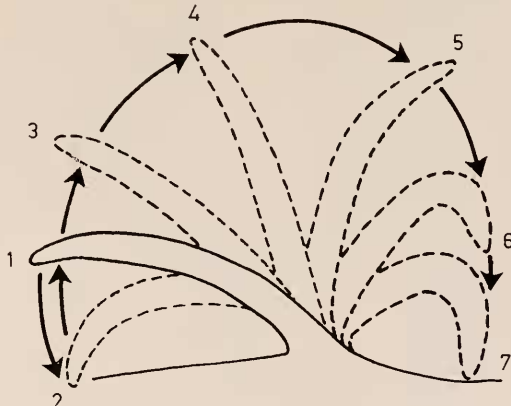


FIGURE 5. *Laternula truncata*, sequential stages in the flicking action of a single siphonal tactile tentacle.

(Fig. 4, SG) which, as suggested by Yonge (1952) for *Entodesma saxicola*, indicates that the periostracum was sticky when secreted and subsequently hardened after the sand grains had adhered. The siphons are capable of total, though slow, retraction. The extensive posterior emargination of the shell valves prevents them from enclosing the siphons. As noted earlier the pallial sinus is deep and broad. The tips of both inhalant (I) and exhalant (E) siphons bear a crown of (a) tactile tentacles (Fig. 4, T) and also possess eyes mounted on special (b) optic tentacles (OT). The exhalant siphon possesses five such eyes whilst the inhalant siphon possesses four. These numbers were constant for all specimens examined. No regular number or order in the arrangement of the tactile tentacles could be recognized, but as a general rule the larger tentacles occupied an outer position. The exhalant aperture closes by contraction at two lines of folding, while the inhalant siphon closes by contraction at five lines of folding. The tentacles are delicately patterned by brown, yellow and white bands, which may be a form of disruptive

coloration, the siphons being difficult to discern against a background of sand grains. The siphons themselves are also camouflaged by the covering of sand grains.

The tactile tentacles of the siphons and to a lesser extent the optic tentacles undergo, at certain times, a curious flicking motion. The resting tentacle (Fig. 5, 1) bends initially outwards (2) and then rapidly flicks inwards towards the siphonal aperture (2-7), flexing as it does so. This process is repeated regularly. It has been established that they perform these flicking motions: (a) just before the siphonal apertures open; (b) immediately after the siphonal apertures closed subsequent to the animal being disturbed; and (c) when the light falling upon the siphons was temporarily obstructed, *i.e.*, a "shadow" reflex; the siphonal apertures also close.

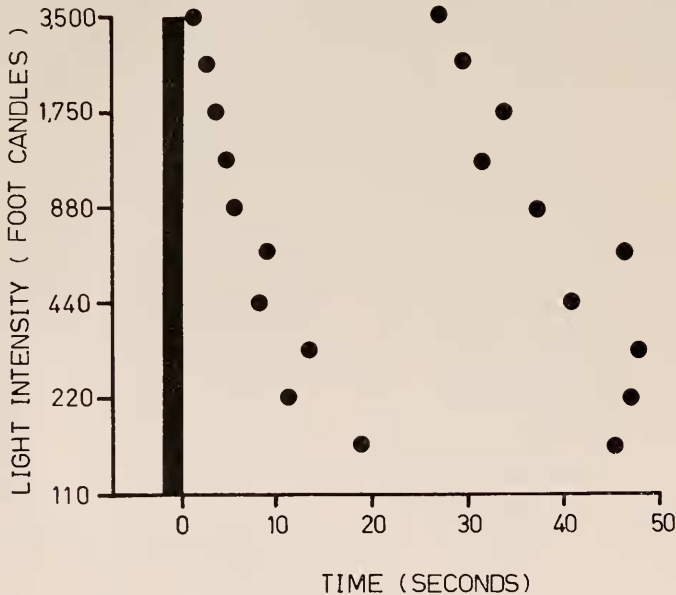


FIGURE 6. *Laternula truncata*, a graph showing the time of onset and the time of cessation at different light intensities, of flicking of the siphonal tentacles after a two second dark phase (the black column). Each point represents the mean of six separate observations.

In the latter case a lag period was observed between the onset of the dark phase and the onset of beating by the tentacles. This was tested experimentally by subjecting individual animals to varying light intensities, measured by means of a Gossen "Lumasix" light meter, and by interfering with the beam of light by cutting off the source for two seconds. The time of (a) the onset of activity and (b) the duration of the period of activity was noted. Figure 6 shows the results of these experiments and demonstrates that with decreasing light intensity the time of onset of the period of activity after a period in the dark was increased, but that the length of the period of activity remained the same whatever the light intensity (approximately thirty seconds). It was further noted that at high light intensities

many more tentacles took part in the beating activity whilst at low intensities the number of participating tentacles decreased. At light intensities below 110 foot candles, no recognizable response was noted. It was finally demonstrated that extension of the dark phase had no effect upon the tentacles; they commenced beating at the same point in time relative to the start of the dark phase as they did after experiencing the dark for only two seconds. It was apparently the onset of darkness, not the termination of darkness, that initiated this activity.

It is possible that the eyes located on the optic tentacles were responsible for detecting the changes in light intensity. A number of bivalves possess pallial eyes.

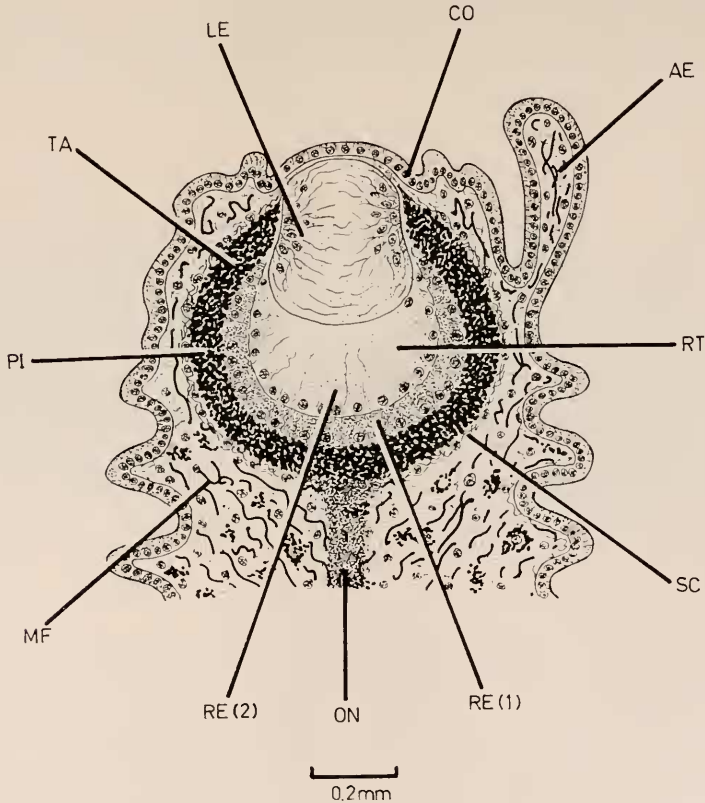


FIGURE 7. *Laternula truncata*, a longitudinal section through an eye located on the tip of an optic tentacle. Abbreviations are: AE, Appendage of the eye; CO, Cornea; LE, Lens; MF, Muscle fibers; ON, Optic nerve; PI, Pigment granules; RE(1), Proximal retina; RE(2), Distal retina; RT, Retinal threads; SC, Sclerotic; TA, Tapetum.

They are perhaps the most well developed in the Pectinacea, *e.g.*, *Pecten* (Dakin, 1910) *Chlamys* and *Amussium* and *Spondylus* (Dakin, 1928). Yonge (1967) has shown that *Pedum spondyloideum* also possesses pallial eyes. In the Cardacea, the cockle *Cardium edule* possesses numerous simple pallial eyes (Barber and Wright, 1969) while *Tridacna* possesses eye-like structures which Yonge (1936) termed

hyaline organs and which were thought to be used for concentrating light upon symbiotic zooxanthellae. Stasek (1966) showed, however, that these structures also possess a sensory function.

Examination of the eyes of *Laternula truncata* in stained section suggests that they are well developed true photoreceptors (Fig. 7). They possess a large lens (LE), lying under a cornea (CO) composed of somewhat flattened cells of the tentacle epithelium. The cup of the eye is composed of three layers which have been named by analogy: (1) An outer sclerotic coat (SC) composed of fibrous material and some muscle fibers. (2) A tapetum (TA) or choroid layer composed of cells containing numerous brown pigment granules (PI). The nuclei of these cells occupy a central or inner peripheral position in the cell. (3) A double retinal layer, in which the proximal layer [Re(1)] is somewhat smaller and darker staining than the distal layer [RE(2)]. The nuclei of these two cell layers are small and

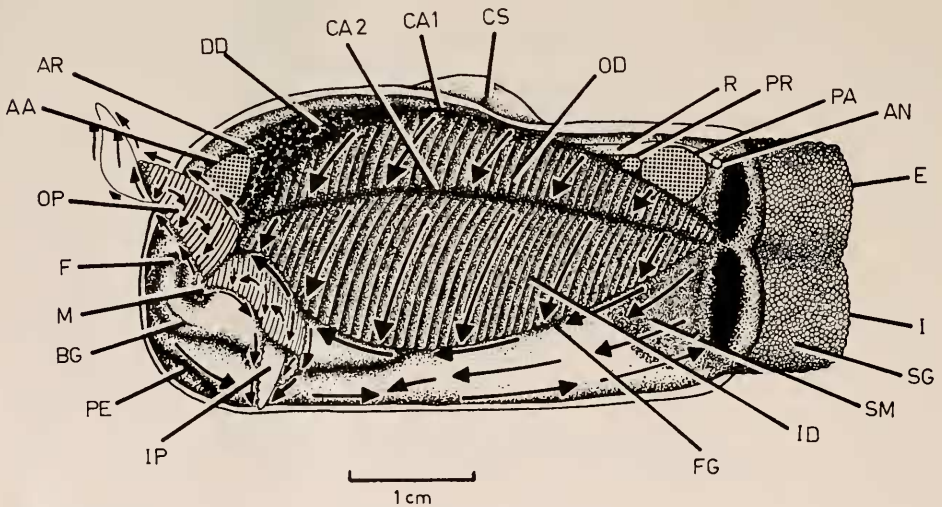


FIGURE 8. *Laternula truncata*, the anatomy and ciliary currents of the organs of the mantle cavity after removal of the left mantle lobe and shell valve. Abbreviations are: AA, Anterior adductor muscle; AN, Anus; AR, Anterior pedal retractor muscle; BG, Byssal groove; CAL, Point of cuticular fusion between the ascending lamella of the outer demibranch and the visceral mass; CA2, Ctenidial axis; CS, Crack in shell; DD, Digestive diverticula; E, Exhalant siphon; F, Foot; FG, Ventral marginal groove; I, Inhalant siphon; ID, Inner demibranch; IP, Inner labial palp; M, Mouth; OD, Outer demibranch; OP, Outer labial palp; PA, Posterior adductor muscle; PE, Pedal gape; PR, Pedal retractor muscle; R, Rectum; SG, Sand grains; SM, Siphonal musculature.

basally situated. The nuclei are thus arranged in two distinct lines. From the innermost layer are directed towards the lens a large number of threads (RT) some of which may represent cell boundaries while others may be fine neurofibrils. No positive result was obtained, however, with Holme's stain for nervous tissue except to identify the optic nerve (ON). From the outer border of the optic tentacle arises a fleshy projection of the epithelium, here termed the eye appendage (AE). No function is as yet attributable to this structure.

The musculature. The anterior and posterior adductor muscles are small (Figs. 1 and 9, AA, PA), the latter somewhat the larger. A similar condition exists in *Clavagella* (Soliman, 1967) and in *Cuspidaria* and *Poromya* (Yonge, 1928). In *Brechites*, the posterior adductor is absent and the anterior adductor is very much reduced (Purchon, 1956). Internally to these two muscles are inserted the anterior (AR) and the posterior (PR) pedal retractors. The latter are very small. These muscles serve to move the foot (F), which in the adult is very small and ineffectual as a digging tool. In *Clavagella*, the foot is very reduced and the pedal retractor muscles absent (Soliman, 1967). The foot of *Laternula truncata* possesses strong ciliary currents and the tip of the foot was often observed between the lips of the mouth, where it may act as an accessory organ for the removal of sediment. A similar habit has been observed in *Dreissena polymorpha* (B. S. Morton, 1969) and *Adula falcata* (Fankboner, 1971).

The foot of *L. truncata* possesses a small byssal groove (Figs. 8 and 9, BG) but there is no functional byssal gland in the adult as there is in *Lyonsia norvegica*

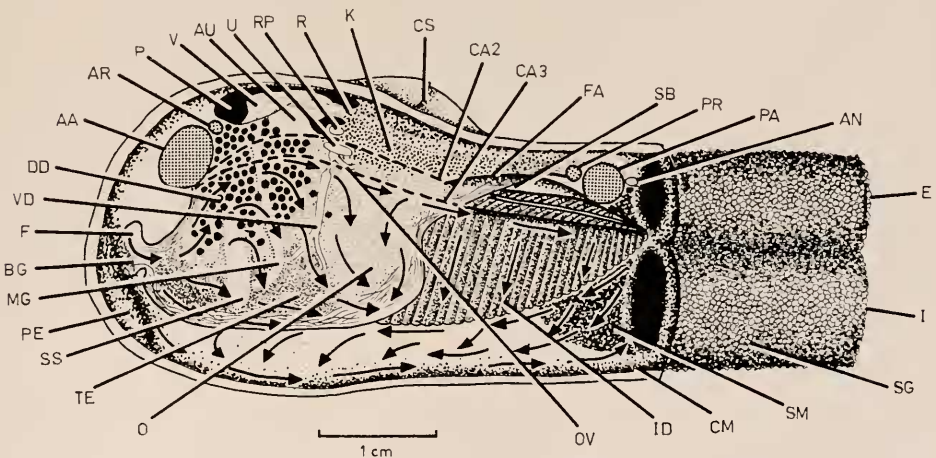


FIGURE 9. *Laternula truncata*, the general anatomy and the ciliary currents of the mantle cavity after removal of the left shell valve, mantle lobe, labial palps and ctenidium. Abbreviations are: AU, Auricle; CA3, Point of cuticular fusion between the ascending lamella of the inner demibranch and the visceral mass; CM, Cut edge of mantle; FA, Free ctenidial axis; K, Kidney; MG, Mid gut; O, Ovary; OV, Oviduct; P, Pericardium; RP, Reno-pericardial aperture; SB, Supra-branchial chambers; SS, Style sac; TE, Testis; U, Urino-genital aperture; V, Ventricle; VD, Vas deferens. (Other abbreviations as in Figure 8.)

(Ansell, 1967) and *Mytilimeria* and *Entodesma* (Yonge, 1952). *Cuspidaria* and *Poromya* (Yonge, 1928) possess a nonfunctional byssal groove.

The ctenidia and labial palps. The ctenidia of *Laternula truncata* comprise two sub-equal demibranchs of which the inner (Fig. 8, ID) is the longer the outer (OD) being considerably reduced.

The upper margin of the ascending lamella of the outer demibranch (CA1) is attached by cuticular fusion to the visceral mass anteriorly and to the dorsal edge of the mantle posteriorly. Cuticular fusions of this type have already been noted by Atkins (1937b) for *Ensis*. The membranous upper margins of the ascend-

ing lamella of the inner demibranchs (Fig. 9, CA3) are attached to the visceral mass by cuticular fusions anteriorly, but posteriorly behind the visceral mass the two demibranchs are united by tissue fusion as in many Leptonacea (Oldfield, 1961; B. S. Morton, 1972). It was noted in some dissected specimens that the marginal membrane of the ascending lamella of the inner demibranch was often separated from the posterior region of the visceral mass. At first it was thought that this separation represented a true aperture on each side of the body, but careful ventral emargination of the shell valves of further specimens and gentle displacement of the ctenidi showed that under natural conditions no aperture exists. Nakazima (1967, 3 pages 149–150) noted a similar condition in *Halicardia* and wrote: "The inner margin of the inner demibranchs is attached to the visceropedal mass by means of a membrane with a rather thick edge. . . . The above described attachment of the inner demibranch is assumed to be so delicate as to be separated with a slight strain. It is, therefore, doubtful whether the junction all along the line (of attachment) is entire or not." This appears true for *L. truncata* although in this species it is thought that the ctenidial/visceral mass junction is not usually separated even though artificial separation only occurs at one place.

Posteriorly an aperture (Fig. 12, 1A) is present in the ctenidial axis (CA2) of both left and right sides. Further posteriorly, behind the visceral mass these apertures unite to form a large Y-shaped cavity.

The ctenidia are flat, heterohabdic, eulamellibranchiate and plicate; the frontal ciliary currents all beat towards the ventral marginal groove (FG) of the inner demibranch and the ctenidia can thus be ascribed to type E (Atkins, 1937a), a condition which is also present in many of the Tellinidae and Semelidae (Atkins, 1937a; Yonge, 1949) as well as other Anatinacea, e.g., *Brechites penis* (Purchon, 1956) and *Entodcsma* and *Mytilimeria* (Yonge, 1952). There is no oralward current in the upper margin of the ascending lamella of either the inner or the outer demibranch.

The number of filaments per plica varied from specimen to specimen. The minimum recorded number from a small animal was 21, while the maximum number recorded was 27. In these two cases there were, respectively, 10 and 13 small filaments on each side of the plica and a single primary filament at the apex. Occasionally two large filaments shared the apex. Inter-filamentar and inter-lamellar junctions are present in both demibranchs.

These particles arriving at the ventral margin of the inner demibranch within the plical trough pass into the ventral groove. Larger particles arriving at this point on the crests of the plicae do not enter the groove. A similar condition has been reported for *Pandora* (Allen, 1954) and *Brechites* (Purchon, 1956). Large, unacceptable particles are removed either by the rejectory currents of the mantle or visceral mass before reaching the labial palps or are removed by the labial palps themselves and subjected to the resorting mechanism of the inner palp surface.

The ctenidial/labial palp junction is of Category 3 (Stasek, 1963) and is thus similar to a wide variety of bivalves with differing habits and with diverse phylogenetic affinities.

The labial palps (Fig. 8, RP, LP) are very long and fulfill the typical sorting function of most lamellibranchs. Material passing over the crests of the palp ridges to the mouth (M) is accepted while material passing to the tips of the palps

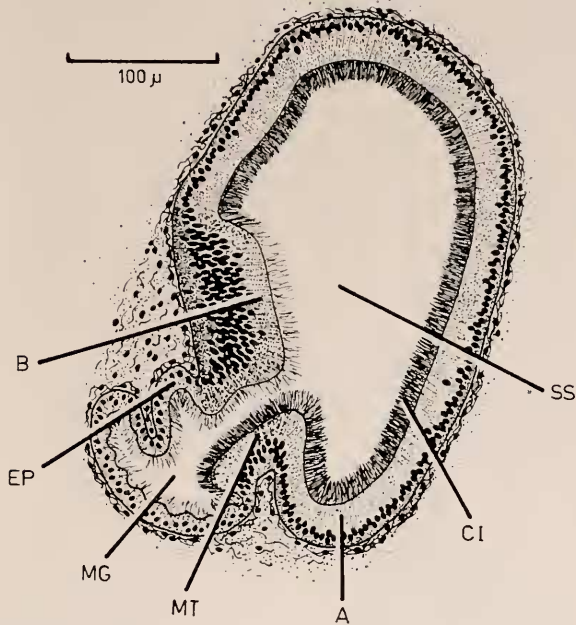


FIGURE 10. *Laternula truncata*, a transverse section through the style sac showing the distribution of the different epithelia. Abbreviations are: A, A cell layer; B, B cell layer; CI, Cilia; EP, Epithelium of mid gut; MG, Mid gut; MT, Minor typhlosole; SS, Style sac.

is rejected and is eventually removed by the rejectory currents of the mantle. Resorting mechanisms for particles of intermediate size also exist on the folds of the labial palps.

The ciliary currents of the mantle and visceral mass. The ciliary currents on the mantle surface serve two major functions. They transport particles from the postero-dorsal regions of the mantle cavity toward the labial palps, thereby acting as acceptor tracts (Figs. 8 and 9). Mid ventrally, however, the cilia of the mantle beat in a posterior direction towards the inhalant siphon. Unwanted material so collected is periodically ejected as pseudofeces.

The ciliary currents of the visceral mass are rather more complicated, but their ultimate effect is to pass material to a mid ventral point. Particles arrive at this point from dorsal and anterior directions, those from the latter coming largely from the foot and from recirculatory currents located antero-dorsally on the visceral mass. Particulate material, upon arrival at the mid-ventral terminus either falls onto the rejectory currents of the mantle or is removed by the ctenidial currents to be ultimately rejected by the mantle. Very similar ciliary currents of both the visceral mass and the mantle have been reported for *Cochlodesma practenuae* (Allen, 1958).

The alimentary canal. The stomach of *Laternula truncata* has been studied by Purchon (1958) and designated as belonging to his Type 4. The present investigation has not revealed any new features of stomach morphology which warrant redescription.

The conjoined style sac and mid gut leaves the stomach at the postero-ventral border and passes ventrally into the visceral mass (Fig. 9, SS). The mid gut (MG) then turns upon itself and travels dorsally to pass through the ventricle (V) and the kidney (Fig. 12, R) terminating in the anus (Fig. 9, AN) behind the posterior adductor muscle. In *Cochlodesma* the rectum passes above the kidney (Allen, 1958).

In transverse section (Fig. 10) the style sac can be seen to comprise a number of distinct epithelial regions. The style sac (SS) itself is bordered by the A and B cell layers. The cells comprising the A cell layer are approximately $18\ \mu$ tall with a dense border of cilia $12\ \mu$ long. The nuclei of these cells occupy a basal position. The cells of the B cell layer (the major typhosole) are approximately $60\ \mu$ tall, with nuclei centrally placed. The sparsely distributed cilia they possess are $15\ \mu$ long. The epithelia bordering the gutter connecting the style sac and mid gut (MG) are of two types. The minor typhosole (MT) is made up of cells $15\ \mu$ tall with basal nuclei and short cilia, $10\ \mu$ long. The remaining layer comprises the cells of the mid gut which are $6\ \mu$ tall with sparsely distributed cilia

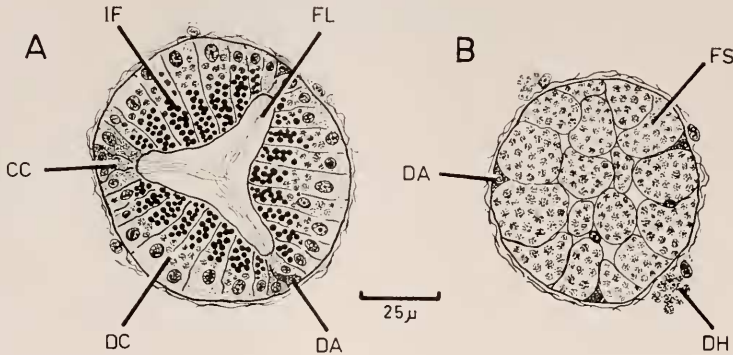


FIGURE 11. *Laternula truncata*, transverse sections through a digestive tubule at (A) the time of absorption and (B) at the time of breakdown. Abbreviations are: CC, Crypt cell; DA, Darkly staining crypt cell; DC, Digestive cell; DH, Digested food material in the haemocoel; FL, Flagella; FS, Fragmentation spherules; IF, Ingested food material.

$10\ \mu$ long. The epithelial zones thus recognized in *L. truncata* comply, in general terms with the zones recognized in other lamellibranchs with a conjoined style sac and mid gut, e.g., *Cardium edule* (B. S. Morton, 1970) and *Venerupis philippinarus* (Kato and Kubomura, 1954).

The digestive diverticula (Fig. 9, DD), surround the stomach and open into the stomach via the left pouch, and via ducts opening directly into the left and right sides of the stomach. The primary and secondary ducts of the diverticula are short and ultimately open into the digestive tubules which bear a very close resemblance to those of tubules which bear a very close resemblance to those of *Cochlodesma* (Allen, 1958) and *Cuspidaria* (Yonge, 1928). The digestive diverticula of different specimens showed a variety of structural conditions. Mature digestive tubules, when seen in transverse section (Fig. 11A) showed that the digestive cells (DC) had ingested very many comparatively large food particles (IF),

(usually) 2–3 μ in diameter, but sometimes as large as 5 μ . The crypt cells (CC) possess flagella (FL) 25 μ long. Small pyramid shaped darkly staining cells (DA) in the crypts resemble those thought by Owen (1970) to be secretory in *Cardium*. Similar cells have been observed in *Halicardia* by Nakazima (1927). Another condition encountered in *L. truncata* was of breakdown (Fig. 11B) both of the digestive cells, to produce large fragmentation spherules (FS), and of the flagellated crypt cells. The small darkly-staining cells in the crypts (DA) alone remained apparently intact. Allen (1958) noted the characteristic large distended

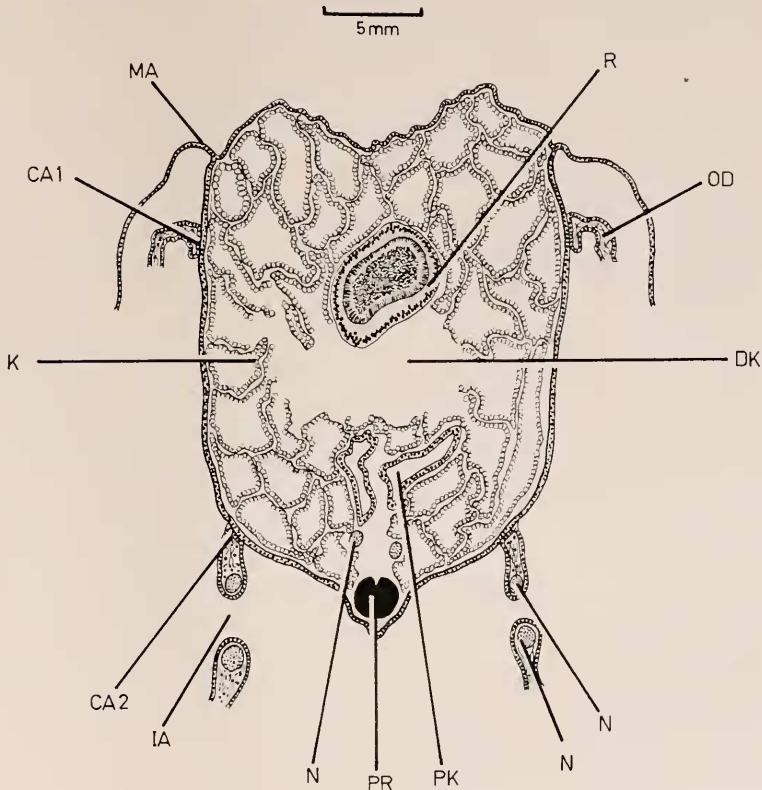


FIGURE 12. *Laternula truncata*, a transverse section through the kidney in the region of the rectum. Abbreviations are: DK, Distal limb of the kidney; IA, Aperture in ctenidial axis; K, Kidney; MA, Mantle; N, Nerve; PK, Proximal limb of the kidney. (Other abbreviations as in Figure 8.)

digestive cells in *Cochlodesma*, but did not appreciate that these cells were probably in the process of breakdown.

The epithelium of the secondary duct which, as in *Cochlodesma* (Allen, 1958), characteristically possesses a brush border also breaks down. During this process large numbers of spherical droplets are budded off within fragmentation spherules from the distal surfaces of the cells. Other droplets are released into the hemocoel

from the bases of the secondary ducts and the digestive tubules (DH). These bear a very close resemblance to the droplets observed within the cells of the kidney.

The pericardium and kidney. The pericardium (Fig. 9, P) lies anterior to the umbo and contains the ventricle (V), which is penetrated by the rectum (R), and two auricles. From the posterior wall of the pericardium a single renopericardial aperture (RP) opens into the kidney (K). The duct leading into the kidney from this aperture is, for a short distance, single, but soon divides into two proximal limbs (Fig. 12, PK). These proximal limbs are extensively ciliated at their origin, but subsequently the cilia are lost and the lumina of the tube increases in size (Fig. 12, PK). The proximal limbs are surrounded by, and posteriorly communicate with the fused lumina of the distal limbs (Fig. 12, DK) of the kidney. The distal limbs communicate with the suprabranchial chamber on each side of the body via a renal aperture which opens into the urino-genital papilla (Fig. 9, U).

The walls of the distal limbs only of the kidney comprise a system of tubules which open into the distal limbs. The cells comprising the tubules possess in different specimens differing amounts of spherical concretions in the free end of the cell. In some specimens the amount was small while in others it was very large.

It has been shown that the pericardial gland of *Dreissena polymorpha* (B. S. Morton, 1969) possesses varying amounts of solid material at different times in relation to the time of feeding. Similar observations have been made by Kowalewsky (1889).

The reproductive system. As in all Anomalodesmata that have been studied, e.g., *Brechites* (Purchon, 1956; 1960), *Laternula truncata* is an hermaphrodite. The testis occupies a ventral position in the visceral mass (Fig. 9, TE) and from each side of the body arises a vas deferens (VD) which passes postero-dorsally. Just before opening into the urino-genital aperture a constriction of the duct occurs, and thereafter the border of the duct is heavily ciliated.

The ovary occupies a dorsal position in the visceral mass (O) and from each side of the body a short oviduct (OV) arises which quickly fuses with the vas deferens. The product of this fusion is a short hermaphrodite duct which opens via a slit-like urino-genital aperture (U) into the supra-branchial chamber. Strong cilia surround the lips of the urino-genital aperture and beat outwards setting up a strong current of water. In all of the Anomalodesmata hitherto studied, e.g., *Cochlodesma* (Allen, 1958) and *Entodesma* and *Mytilimeria* (Yonge, 1952) the gonads open by separate ducts, which also open separately from the renal aperture. The condition existing in *L. truncata* is therefore unusual.

DISCUSSION

The Anomalodesmata comprise a diverse assemblage of little known bivalves. The most well known superfamily, the Pandoracea of which the Laternulidae are a family, are all adapted to a sedentary mode of life living intertidally or sublittorally in sandy deposits. Some of them, e.g., *Lyonsia* (Ansell, 1967) and *Entodesma* (Yonge, 1952) possess a functional byssal gland. This organ, in adult, *Laternula* is reduced to a non-functional byssal groove. In the Poromyacea, *Cuspidaria* and *Poromya* also possess non-functional byssal grooves (Yonge, 1928). In the adult *Laternula truncata* the reduced foot is probably used as an accessory mantle cleansing organ, although in the young animal it is used for burrowing.

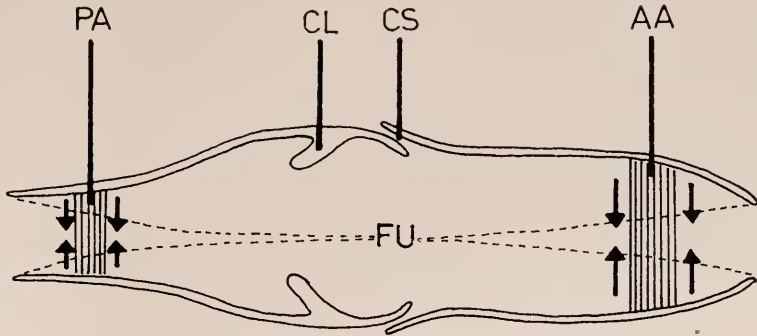


FIGURE 13. *Laternula truncata*, a horizontal section through the shell to demonstrate the method of movement of the shell valves. Abbreviations are: AA, Anterior adductor muscle; CL, Clavicle; CS, Crack in shell; FU, Fulcrum; PA, Posterior adductor muscle.

The microstructure of the shell of the Pandoracea is most similar to that of the Poromyacea (Taylor *et al.*, 1972). The thinness of the shell in *L. truncata* in particular and in the Pandoracea in general (Taylor, *et al.*, 1972) possibly represents another step in the trend of this group towards a sedentary mode of life. The thinness of the shell in *L. truncata* has necessitated the development of a clavicle or strengthening strut for each shell valve. Such a system is not designed to protect the animal from external damage, but from the internal compression forces created by the adductor muscles. A further modification has been the development of a lithodesma which effectively fixes the ligament, thereby preventing the shell valves from opening under the pressure exerted principally by the primary ligament and by the secondary ligament of fused periostracum. The secondary ligament is also found in other genera of the Pandoracea, *e.g.*, *Pandora* and *Cochlodesma* (Allen, 1954; 1958) and *Entodesma* and *Mytilimeria* (Yonge, 1952) although only in the latter two genera is there a lithodesma. A lithodesma occurs in *Mydora*, *Myochama* and *Chamostrca* (Thiele, 1935), and in *Thracia* (Tebble, 1966). The trend in the Pandoracea towards the relative immobilization of the ligament by means of a lithodesma has resulted in *L. truncata* in the adductor muscles being relatively small and ineffectual. This is especially true of the posterior adductor. The pedal retractors of the adult are similarly very small.

It would thus seem that shell movements in *Laternula* (Fig. 13) are small and are brought about by the contraction of (1) the anterior and posterior adductor muscles (AA, PA) and (2) the orbital muscles acting against the fulcrum (FU) formed by the meeting of the shell valves dorsally and ventrally in the mid line only. The muscles act in opposition, not as in the typical bivalve to the ligament but to the flexibility of the shell itself. The flexibility of the shell is enhanced by the median crack (CS) in each of the shell valves which allows this action to occur, without putting excessive strain upon the fragile shell. The clavicles (CL) give added strength to the shell. Significantly, *Cochlodesma practenue* also possesses a crack in the shell (Tebble, 1966).

It is envisaged that this trend towards the fixation of the shell in the Laternulidae has proceeded further in the Clavagellacea (Soliman, 1967; Purchon, 1956) and

has resulted in the total fixation of the shell by the development of an adventitious shell and the adoption of muscular pumping as a means of burrowing and possibly of collecting food material. Significantly the muscles which perform this action are greatly enlarged orbital muscles (Purchon, 1960). There is only a small anterior adductor muscle remaining in *Brechites* (Purchon, 1958) and significantly the shell valves are free when young (Taylor *et al.*, 1972). In the Saxicavacea (Yonge, 1971) also, the greatly enlarged orbital muscles are used in the movement of the shell valves.

The siphons of *L. truncata* possess numerous tactile tentacles and nine optic tentacles. The optic tentacles have been shown to possess true eyes. Such true eyes are unusual, especially since well developed eyes are usually only found [exceptions being *Pedum spondyloideum* (Yonge, 1967) and *Spondylus* (Dakin, 1928)] in free living bivalves, *e.g.*, the Pectinacea (Dakin, 1910, 1928). Charles (1966) has stated that the eyes of the Bivalvia cannot be related to any development from a basic plan, as can most of the gastropod eyes. The eyes of *Cardium* (Barber and Wright, 1969) are very simple and do not even possess a lens. The eyes of *L. truncata* on the other hand, are possibly as advanced as those of the Pectinacea, especially since there is a double retina, as in *Pecten* (Schlicher, 1926). In other respects also the eyes of the two animals are very similar and the sheet-like layers of the lens of *L. truncata* may suggest an even greater refinement in this species.

In *L. truncata*, the eyes detect subtle changes in light intensity and it is thought that they constitute the receptive portion of a reflex arc the efferent response of which is the curious flicking motions of the tactile tentacles. The shadow reflex recorded for *L. truncata* can be equated with the primary "off" response demonstrated for *Cardium edule* (Barber and Land, 1967), *Pecten* (Land, 1966) and *Onchidium* (Fujimoto, Yanase, Okumo and Iwata, 1966) and coincidental with a fall in light intensity. Such a response would strongly suggest therefore that the distal retina of the eye of *L. truncata*, at least, is a ciliary photoreceptive structure since an "off" response is not associated with a rhabdomal receptor cell. This "shadow" reflex noted for example by Sharp (1883) in *Solen* has subsequently been observed in other bivalves, *e.g.*, *Spisula* (Kennedy, 1960) and *Tridacna* (Stasek, 1965) and in most cases resulted in withdrawal of the siphon. It must therefore be regarded as constituting a defensive reflex in most bivalves.

It is thought that the flicking of the tactile tentacles of *L. truncata* may serve a number of functions. The tentacles flick just prior to siphonal withdrawal, an action which perhaps constitutes a defensive response, concealing the outline of the sand covered siphons by bringing other particles over them. A comparable behavior pattern occurs in certain flatfish when they settle on the surface of the sand, by flicking sand particles over them to break up their outline. The flicking action of the tentacles in *L. truncata* just before the siphons reopen in all probability clears the sand away prior to the emergence of the siphons and the resumption of feeding. The "shadow" reflex is unusual, however, since it is accompanied by closure of the siphonal aperture but not by siphonal withdrawal and cannot thus be regarded as a defensive reflex. To the contrary such an action would only serve to attract the attention of predators. The resting tentacles are cryptically covered and the siphonal covering of adhered sand grains make the

animal impossible to see, at least to the human eye, in its natural environment. Mangroves are characteristically the feeding grounds of a large number of permanent and migratory wading birds. Such animals wade along the shoreline seeking food. A quiescent and camouflaged *L. truncata* would possibly escape detection, but would cleanse itself of the disturbed sediments kicked up by the bird once this (and its shadow) had passed. Perhaps too it capitalizes on the detritus kicked up by the bird. Such a feeding mechanism, though unproven, is a distinct possibility. *L. truncata* may thus be regarded as a specialized detritus/suspension feeder, collecting material raised into suspension as a result of extraneous disturbance. Within the mantle cavity the organs concerned with the collection, sorting and either acceptance or rejection of this material are well developed. The ctenidia are plicate, passing food material into the ventral marginal food groove of the inner demibranch only. The labial palps of many of the deposit feeding Tellinacea, e.g., *Abra alba* (Yonge, 1949) and the rejectory tracts of the mantle and visceral mass are efficient. The foot probably acts as an accessory cleansing organ. The organs of the mantle cavity are thus typical of deposit feeding bivalves.

The digestive tubules of *Laternula* are similar to those of *Cochlodesma* (Allen, 1958) and *Cuspidaria* (Yonge, 1928). It has been demonstrated for *Laternula kamakurana* by Nakazima (1955) and in this study of *L. truncata* that the digestive cells are capable of ingesting comparatively large particles, e.g., (2-5 μ), as in *Cuspidaria* (Yonge, 1928). Characteristically small particles only are ingested by the majority of bivalves; *Teredo* (Yonge, 1926) and *Nuculana* (Yonge, 1939) being exceptions in the possession of "specialized" diverticula for the ingestion of comparatively large particles. According to Owen (1956) the digestive diverticula of the Nuculidae are not absorptive but are secretory in function.

L. truncata is a simultaneous hermaphrodite, as apparently are all other members of the Pandoracea and Clavagellacea. Unlike the other Pandoracea, however, the testis, ovary and the excretory aperture of *L. truncata* open into a common urinogenital papilla. Such a modification, if one accepts that the hermaphroditic condition is characteristic of specialized bivalves as suggested by Purchon (1968), must represent an even greater specialization in this species.

Taylor, *et al.* (1972) suggest that the Clavagellacea and Poromyacea have a close affinity with the Pandoracea, and further suggest that all of these lineages arise from a Pholadomyacean stock in the Trias or lower Jurassic. Runnegar (1972) has attempted to elucidate the morphology of *Pholadomya candida* based upon an examination of the shell. There can be little doubt that it would be highly profitable to examine a living *Pholadomya* and perhaps so to shed some light on the evolution of the Anomalodesmata. The morphological eccentricities of *L. truncata*, though largely of a specialized nature and highlighting the success of the Pandoracea in general also seem to foreshadow the extreme morphological specialization of the Clavagellacea.

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SUMMARY

Laternula truncata (Lamarck) is a highly specialized member of a somewhat diverse assemblage of bivalves, the Anomalodesmata. It is found buried in coarse sand on the seaward side of mangrove formations in South East Asia. (1) The shell is thin and possesses a lithodesma, which effectively prevents the opening of the shell in the typical bivalve manner. Movement of the shell is achieved by the bending of the dorsal margin of the shell at a dorso-ventral crack in each shell valve and by the flexibility of the shell itself. Ventral orbital muscles are probably as important in valve movements as are the reduced adductors. A strengthening strut or clavicle is present on each valve. (2) Mantle fusions are of type B ventrally, and type C dorsally. There is a small pedal gape, but no fourth pallial aperture. (3) The siphons which are of type C, are covered in sand grains. At their tips they possess tactile tentacles and optic tentacles; the structure of the complex eyes which the latter possess are described. The tactile tentacles undergo unusual flicking motions when a shadow falls over the siphons. This may be a defensive and a cleansing response and also play a role in feeding. (4) The ctenidia are plicate and heterorhabdic and have ciliary currents of type E (Atkins, 1937a). The outer demibranch is reduced, and the ctenidial axis possesses an aperture on each side of the body which unite posteriorly to form a Y-shaped cavity. (5) The ctenidial/labial junction is of type 3 (Stasek, 1963), and the labial palps are large. (6) The stomach is of type 4 (Purchon, 1958). The structure of the style sac and the digestive diverticula are described. (7) The structure of the kidney is described. (8) The reproductive system is described. *L. truncata* is hermaphrodite and the oviduct, vas deferens and urinary duct open, unusually, via a common urinogenital aperture. Many of the morphological adaptations of *L. truncata* foreshadow the highly specialized condition in the Clavagellacea.

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